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CONSERVATION IMPLICATIONS OF GENETIC VARIATION IN THREE RARE SPECIES ENDEMIC TO FLORIDA ROSEMARY SCRUB¹

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Habitat conversion and fire suppression during the last 50 yr have greatly reduced and altered Florida scrub vegetation, resulting in threats to the persistence of its unique flora. As part of a larger conservation project, we investigated patterns of isozyme variation in three rare perennial scrub plants with overlapping ranges endemic to Florida rosemary scrub on the Lake Wales Ridge. All three species have low levels of genetic variation, comparable to or lower than those generally reported for rare plants with restricted geographic ranges. *Liatris ohlingerae* has more than twice the expected heterozygosity of the other two species, with little population differentiation. In contrast, *Hypericum cumulicola* has highly differentiated populations with little apparent interpopulation gene flow and heterozygote deficiencies indicative of inbreeding. *Eryngium cuneifolium*, the species with the narrowest range and fewest populations, has intermediate values for genetic parameters. Although the three species have narrow and overlapping geographic ranges and similar habitat specificity, we discuss how optimal conservation of each species differs.

Key words: conservation; Florida scrub; genetic variation; isozyme analysis; Lake Wales Ridge; rare plants; rosemary scrub.

Integrated conservation planning using autecology, demography, and genetic diversity data provides the greatest chance of assuring the long-term survival of rare and endangered species. We are taking this approach in research and conservation of a little-studied suite of rare plants of the Lake Wales Ridge (LWR) and adjacent ridges in central Florida. This paper compares patterns of distribution of genetic variation in *Eryngium cuneifolium* Small (Apiaceae), *Hypericum cumulicola* (Small) P. Adams (Hypericaceae), and *Liatris ohlingerae* (Blake) B. L. Robins (Asteraceae). Although all three are federally listed endangered endemics of extremely restricted geographic range with narrow habitat specificity, they differ in population size and population numbers (Table 1), range (Fig. 1), response to fire, and other traits. Data from this study, along with additional studies of pollinators, breeding systems, and demography, will contribute to a comprehensive multispecies conservation strategy.

All three species are restricted to the ecologically imperiled Florida scrub community (Christman and Judd, 1990). This habitat supports 26 plants that are listed as threatened

or endangered, 22 of which are restricted to central peninsular Florida in the LWR and vicinity (USFWS, 1995). This high concentration of rare plants accounts in great part for the identification of peninsular Florida as one of the three areas of greatest endemism in the United States (Dobson et al., 1997). The antiquity of scrub vegetation, estimated to have survived since the Pliocene without major climatic disruption (Watts and Hansen, 1994), is most often cited as the cause of the high levels of endemism. There is also genetic evidence of isopatric speciation promoted by isolation of scrub habitats in island archipelagos separated from the mainland during periods of high sea level (e.g., Lewis and Crawford, 1995).

Florida scrub is a xeric, shrub-dominated ecosystem found on nutrient-poor soils (Myers, 1990; Menges, 1998). Dominant species include oaks, ericads, and dwarf palms (Abrahamson et al., 1984). Scrub of the LWR occurs in a mosaic of wetlands, flatwoods, and sandhill vegetation. Habitat conversion for citrus groves, residential development, and other land uses has reduced LWR scrub habitat over 90%, mostly during the last 50 yr (Peroni and Abrahamson, 1985). In addition to the direct impact of habitat loss, fire suppression has altered species composition in scrub communities (e.g., Menges and Kohfeldt, 1995; Abrahamson and Abrahamson, 1996).

Eryngium cuneifolium and *Hypericum cumulicola* are restricted to open areas of well-drained white sand in rosemary scrub (a subtype of scrub dominated by Florida rosemary (*Ceratiola ericoides*) that is very xeric with more persistent gaps (Hawkes and Menges, 1996) and longer fire return interval than other types of scrub (Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernandes, 1997). *Eryngium cuneifolium* occurs in an area 31 km N–S in southern Highlands County with one

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TABLE 1. Population characteristics of three rare plants of the Lake Wales Ridge.

Species	No. pops. surveyed	Median pop. size (N) ^a	Median pop. area (m ²)	Mean density (no. plants/m ²)
<i>Eryngium cuneifolium</i>	16	4280	5425	1.84
<i>Hypericum cumulicola</i>	34	539	8750	0.46
<i>Liatris ohlingerae</i>	30	170	3634	0.19

^a Population defined as 50 m from other patches.

isolated population in central Highlands 15 km disjunct from the nearest other population (Fig. 1). *Hypericum cumulicola* is somewhat wider ranging with scattered populations along the LWR in Polk and Highlands Counties (Fig. 1) and an isolated population in Polk County, off the LWR. *Eryngium cuneifolium* and *H. cumulicola* mostly occur in discrete populations separated by large areas of unsuitable habitat (Quintana-Ascencio and Menges, 1996). *Liatris ohlingerae* grows in rosemary scrub and scrubby flatwoods in Highlands and Polk Counties

(with an isolated occurrence off the LWR in Polk County; Fig. 1). Scrubby flatwoods have smaller, less-persistent gaps and a shorter fire return interval than rosemary scrub (Menges and Hawkes, in press). *Liatris ohlingerae* does not appear to specialize in open microsites.

MATERIALS AND METHODS

Study species—All three species are thought to be distinct taxonomically (Wunderlin, 1998). *Eryngium cuneifolium*, wedge-leaved button-

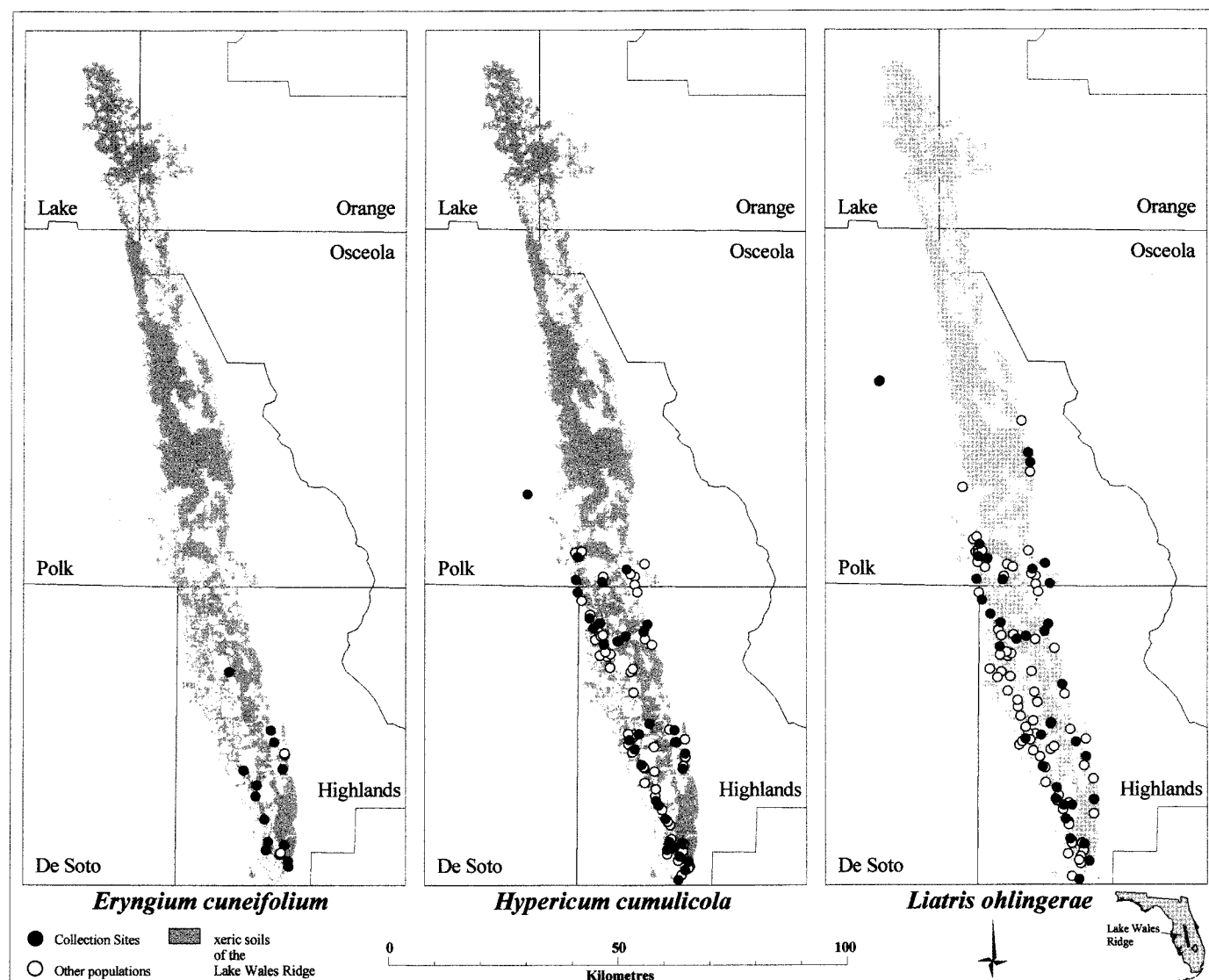


Fig. 1. Known localities and populations sampled for the three species in this study. Not all populations are visible as distinct dots at this scale.

TABLE 2. Enzyme systems studied, with number of loci scored, for each species. Numbers in parentheses following system names are Enzyme Commission designations.

Enzyme system	<i>Eryngium cuneifolium</i>	<i>Hypericum cumulicola</i>	<i>Liatris ohlingerae</i>	Abbreviation
Acid phosphatase (3.1.3.2)	—	—	1	ACP
Aconitase (4.2.1.3)	3	2	1	ACO
Alcohol dehydrogenase (1.1.1.1)	1	3	1	ADH
Aldolase (4.1.2.13)	1	—	—	ALD
Aspartate aminotransferase (2.6.1.1)	2	—	—	AAT
Fluorescent esterase (3.1.1.—)	2	—	—	FES
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	2	1	1	G3P
Isocitrate dehydrogenase (1.1.1.41)	1	1	—	IDH
Malate dehydrogenase (1.1.1.37)	3	3	1	MDH
Menadione reductase (1.6.99.—)	2	2	1	MNR
Phosphoglucomutase (5.4.2.2)	2	2	1	PGM
Phosphoglucose isomerase (5.3.1.9)	—	3	2	PGI
6-phosphogluconate dehydrogenase (1.1.1.44)	2	1	1	6PG
Triosephosphate isomerase (5.3.1.1)	—	—	2	TPI
Total number of loci	21	18	12	

snakeroot, is a caespitose, taprooted perennial herb with diffusely branching flower stalks 0.25–0.50 m tall. Dispersal appears to be primarily via gravity, with most seedlings found clustered about the last season's flowering plants.

Demographic and spatial patterns in *E. cuneifolium* are strongly influenced by fire (Menges and Kimmich, 1996). Fire kills most established individuals, although some resprout from taproots. Postfire recruitment from a persistent seed bank (Quintana-Ascencio, 1997) can be substantial. Populations decline between fires concomitant with growth of dominant shrubs (Menges and Kimmich, 1996).

Hypericum cumulicola, the Highlands scrub hypericum, is a perennial herb ranging from 20 to 70 cm in height. Small, yellow, bisexual flowers are produced from April through November. Fruits are small capsules producing 19 ± 4 seeds ~0.5 mm in size.

Hypericum cumulicola plants do not survive fire (Menges and Kohfeldt, 1995); population recovery requires the recruitment of seeds from a seed bank or dispersal from nearby populations (Menges and Kohfeldt, 1995). Relationships between demographic patterns and time since fire are somewhat more complicated in *Hypericum cumulicola* than in *Eryngium cuneifolium*, although survival and growth are greatest in recently burned patches (Quintana-Ascencio, 1997; Quintana-Ascencio and Morales-Hernandez, 1997). Not all patches of rosemary scrub suitable for growth and reproduction of *H. cumulicola* are occupied by this species (Quintana-Ascencio, Dolan, and Menges, 1998). Hence *H. cumulicola*, along with *E. cuneifolium*, exhibits patchy distribution patterns consistent with metapopulation dynamics (Quintana-Ascencio and Menges, 1996).

Liatris ohlingerae, scrub blazing star, is an herb with a perennating corm. Peak flowering is June–August, with seed heads maturing from late July through October. Achenes are 8–9 mm long and densely pubescent with a plumose pappus 5–6 mm long. Postfire resprouting of *L. ohlingerae* provides most of its recovery (Menges and Kohfeldt, 1995), while seedling recruitment is temporally and spatially patchy and seedling growth slow.

Liatris ohlingerae populations are generally small, with scattered plants at low densities over large areas. Because of its resprouting and slow growth, it is likely that its populations fluctuate to a lesser extent than the other two species.

Sample collection and population size estimates—Populations from across the geographic range of each species were selected for genetic study (Fig. 1). For isozyme sampling and population size estimates, populations were defined as plants occurring within 50 m of each other.

No populations within 1.6 km of another sampled population were included in our genetic study. Within populations, either leaves or stem tips with flowers (depending on the species, see below) were collected for isozyme analysis from at least ten and where possible 30 plants from throughout the population. In this way, if genetic substructuring existed, plants were sampled across neighborhoods to maximize detection of variation. Leaves or buds were stored in plastic bags on ice and shipped overnight to Butler University.

Population size was assessed by direct counts in smaller populations (generally, populations of 150 or less) and assessed by counting subsamples in larger populations. Counts were generally made within belt transects 2 m wide (4 m for *L. ohlingerae*) running lengthwise through the long axis of populations, beginning at stratified random points. The dimensions of the populations were estimated in the field or digitized from aerial photographs. Count subsamples were extrapolated to estimates of population size by extrapolating from the total transect area to the estimated population area.

Electrophoresis and data analysis—Leaves were assayed for *E. cuneifolium* and *L. ohlingerae* and flower buds for *H. cumulicola*. Few loci could be resolved from *H. cumulicola* leaves. The modified sorghum buffer of Morden, Doebley and Schertz (1987) was used for extraction. Standard procedures for starch gel electrophoresis were conducted with recipes following Dolan (1994, 1995), with the exception that flowers of *H. cumulicola* were ground in extraction buffer and centrifuged for 3 min at 3000 rpm before being wicked onto chromatography paper. Enzyme systems scored for each species are in Table 2. Allelic assignments were based on the observed pattern of population variation, the known subunit structure of the enzymes, and the cellular compartmentalization generally observed for plant enzymes (Kephart, 1990).

Data were analyzed using the Biosys-1 software of Swofford and Selander (1989). Allele frequency data and details of laboratory procedures are available from Dolan. Standard measures of levels of genetic variation (percentage of loci polymorphic, number of alleles per locus, and observed and expected heterozygosity) were calculated for populations and for species as a whole. Wright's *F* statistics were calculated for all loci, and deviations from Hardy-Weinberg equilibrium were detected using standard goodness-of-fit chi-square tests for variable loci. Interpopulation gene flow (*Nm*) was estimated from population differentiation data (Wright, 1951).

RESULTS

Levels of genetic variation—*Hypericum cumulicola* had low values for percentage of loci polymorphic and

TABLE 3. Comparison of isozyme variation in three rare plant endemics of the Lake Wales Ridge, with narrow endemic plants surveyed by Godt and Hamrick (1996). Numbers in parentheses are standard errors.

	<i>Eryngium cuneifolium</i>	<i>Hypericum cumulicola</i>	<i>Liatris ohlingerae</i>	Endemics ^a
No. extant pops. ^b	20	90	115	—
No. of pops surveyed	16	34	30	—
No. of loci	21	18	12	—
Mean no. plants/locus	30.0	28.1	22.0	—
Species-level % loci polymorphic	43.8	28.0	50.0	43.8
Population-level ^c % loci polymorphic	16.0 (1.6)	6.2 (0.9)	31.4 (1.4)	29.2
Mean no. alleles/polymorphic locus	1.61 (0.05)	1.25 (0.03)	1.93 (0.06)	2.6
Obs. heterozygosity	0.041 (0.004)	0.006 (0.001)	0.095 (0.005)	—
Exp. heterozygosity	0.054 (0.004)	0.023 (0.003)	0.121 (0.005)	0.074
Mean Nei's genetic identity	0.954	0.937	0.987	
Estimated gene flow (Nm^d)	0.31	0.09	1.83	

^a Cited in Godt and Hamrick (1996).^b Based on databases of the Florida Natural Areas Inventory and field surveys.^c Averaged across all populations.^d Calculated as $Nm = \{(1/F_{ST}) - 1\}/4$, from Wright (1951) (assumes equilibrium conditions).

the more integrative measure, expected heterozygosity (Table 3). This species differs from the other two in having a very large F_{ST} value of 0.73, indicating a large degree of differentiation between populations (Table 4). The species with the greatest amount of variation is *L. ohlingerae*. This plant also exhibited very low population differentiation. *Eryngium cuneifolium*, the species with the fewest populations, had intermediate values for all measures.

TABLE 4. Summary of F statistics at all loci for each species.

	Locus	F_{IS}	F_{IT}	F_{ST}
<i>Eryngium cuneifolium</i>	6PG-2	0.649	0.658	0.025
	MDH-3	0.191	0.498	0.380
	PGM-1	-0.193	0.371	0.473
	ADH-1	-0.067	0.153	0.206
	FES-1	-0.102	0.691	0.719
	FES-2	-0.018	0.001	0.017
	MNR-2	0.498	0.527	0.057
	IDH-1	0.371	0.402	0.049
	ALD-1	0.766	0.940	0.743
	ACO-1	-0.018	-0.001	0.017
	Mean	0.078	0.488	0.445
<i>Hypericum cumulicola</i>	MNR-2	0.702	0.874	0.576
	6PG-1	0.715	0.964	0.873
	MDH-1	0.729	0.909	0.663
	MDH-3	0.717	0.930	0.753
	IDH-1	0.889	0.946	0.512
	Mean	0.729	0.927	0.730
<i>Liatris ohlingerae</i>	ADH-1	-0.157	-0.043	0.099
	PGI-1	0.126	0.222	0.110
	PGI-2	0.310	0.407	0.141
	PGM-1	0.009	0.114	0.105
	TPI-1	-0.069	-0.006	0.059
	TPI-2	0.046	0.146	0.105
	Mean	0.144	0.246	0.120

Estimated levels of interpopulation gene flow (Nm) and genetic identity—*Liatris ohlingerae* had the highest levels of gene flow, almost two individuals per generation (Table 3). We found an extremely small Nm value (<0.1) for *H. cumulicola*, indicating virtually no interpopulation gene flow. *Eryngium cuneifolium* had an intermediate Nm value of 0.31. Despite the range in gene flow estimates, populations within each species were very similar to each other, with Nei's genetic identity values ranging from 0.937 to 0.987 (Table 3).

Inbreeding coefficients, fixation indices, and deviations from Hardy-Weinberg equilibrium—Inbreeding, as indicated by a positive F_{IS} value of 0.729, is very high in *H. cumulicola*. F_{IS} values are much lower for the other two species (Table 4). The number of loci not in Hardy-Weinberg equilibrium (HWE) also differed among the species. For *E. cuneifolium*, 24 significant deviations were detected among 69 possible (34.8%). Six significant fixation indices were negative, indicating an excess of heterozygotes. Eighteen cases of heterozygote deficit were found.

For *H. cumulicola*, all but three possible cases deviated from HWE (37/40 or 92.5%). For *L. ohlingerae*, 17 of 166 (15%) of possible cases deviated from HWE. All of the deviations for these two species were the result of significant heterozygote deficiencies, providing evidence of inbreeding.

DISCUSSION

General patterns of isozyme variation—All three species studied have lower levels of variation for all measured parameters than those generally reported for seed plants, but values for *E. cuneifolium* and *L. ohlingerae* are comparable to those reported for endemic species (Table 3). Population-level values for percentage loci poly-

morphic (6.2%) and average number of alleles per polymorphic locus (1.25) are very low for *H. cumulicola*.

Liatris ohlingerae, the species with the greatest potential for long-distance seed dispersal, has the highest levels of genetic variation, the fewest loci deviating from Hardy-Weinberg equilibrium, and the lowest level of differentiation between populations of the three species in our study. These characteristics are all consistent with high gene flow. Populations of *L. ohlingerae* consist of relatively few plants, but cover large areas. Occasionally, widely separated lone plants are found. Unlike *E. cuneifolium* and *H. cumulicola*, which are restricted to isolated islands of xeric, open rosemary scrub, *L. ohlingerae* also can occur in the matrix of lower oak scrub (scrubby flatwoods) that surrounds these rosemary scrub islands. Populations are less straightforward to distinguish in the field and may not be as physically distinct as those of *E. cuneifolium* and *H. cumulicola*. This pattern of spatial dispersion of populations, along with reasonably high rates of seed and pollen movement, may account in large part for the low level of genetic differentiation among populations. In addition, high levels of genetic variation are consistent with relatively stable population dynamics, including long individual life and resprouting following fire.

Hypericum cumulicola has the most limited genetic variation of the three species studied. Most of that variation is found among populations with almost no detectable gene flow. The genetic structure of these populations is in close accord with the spatial distribution of plants. Populations are isolated in almost every case by unsuitable intervening habitat types, creating small islands of suitable, occupied rosemary scrub and locally abundant, relatively dense populations.

The apparently high rates of inbreeding (demonstrated by heterozygote deficit and high F_{IS} values) found in this study were supported by Quintana-Ascencio, Dolan, and Menges (1998) in field transplant experiments designed to demonstrate the potential for metapopulations in the species. Seedlings of *H. cumulicola* survived and reproduced in apparently suitable but previously unoccupied habitat. Screening of the transplant's isozyme genotypes and monitoring of seedling genotypes revealed no gene flow over distances >1–2 m.

An alternative explanation for heterozygote deficit and high F_{IS} values is spatial structuring of genetic variation within populations. If gene flow is limited, genetic neighborhoods with different allele frequencies will result in detection of deficiencies in heterozygotes when entire populations are sampled. We are exploring this possibility in *H. cumulicola* with additional studies.

Eryngium cuneifolium has intermediate values for most genetic parameters. The observed moderate levels of population differentiation may be maintained by fire-dependent demographic fluctuations (Menges and Kimmich, 1996), with bottlenecks or even local extirpations in aboveground populations in areas that have persisted without fires for >20 yr. However, *H. cumulicola*, with its high degree of population differentiation, shares this demographic pattern. Population sizes (Table 1) and population-level genetic diversity (Table 3) are much greater in *E. cuneifolium*. This may reflect the species' ability to

recover population numbers more quickly following bottlenecks, limiting their negative genetic effects.

Isozyme variation in *Eryngium cuneifolium* was also studied by McDonald and Hamrick (1996) during a survey of scrub plants with different scales of endemism. They assayed 31 loci from only two populations. Their two populations were also sampled in our study. They detected lower levels of genetic variation at the species level for percentage of loci polymorphic, 32.0 vs. the 48.0% reported here. Population-level values were more comparable (29.0% of loci polymorphic vs. 16.0% in our study, 2.0 alleles/polymorphic locus vs. 1.6 in our study and expected heterozygosity of 0.086 in McDonald and Hamrick's study vs. 0.054 in ours). McDonald and Hamrick (1996) found most loci they examined in *E. cuneifolium* to be close to HWE, but in our larger study, we found deficiencies of heterozygotes.

Conservation implications—Studies of other herbaceous Florida scrub endemic plants have found high levels of genetic variation or distinct patterns of spatial organization, although Godt, Race, and Hamrick (1997) recently reported low levels of within-population variation in a LWR endemic clonal shrub taxon). Lewis and Crawford (1995) found scrub endemic *Polygonella* species to have higher levels of genetic variation than their widespread congeners. They stressed the significance of remnant populations as reservoirs of variation in the genus, which may have survived Pleistocene sea level rises and range restrictions in a scrub bioregion. In addition, metapopulation models based on detailed demographic, dispersal, and distribution data suggest that the Florida scrub-jay exists as 42 distinct metapopulations, each characterized by some degree of isolation. Only half of these populations are described as viable (Stith et al., 1996).

An annual scrub endemic, *Warea carteri*, has clines in allele frequencies along the north-south axis of the LWR (Evans et al., in press), reflecting genetic structure. Likewise, McDonald and Hamrick (1996) found biogeographic patterns of unique alleles in *Ceratiola ericoides*, a plant commonly found in scrub throughout Florida. Differences between populations were also detected by McDonald and Hamrick (1996) in species of the much more geographically restricted LWR endemic genus *Dicerandra* (most differences were across species because a very small number of populations were sampled). These data show that scrub patches are not all equal from a genetic perspective and support the need for preservation of multiple patches of scrub from across the Florida peninsula, as well as the preservation of separate scrub patches within the LWR to preserve genetic integrity. Optimum conservation for each of our study species requires the preservation of current or historic populations and suitable currently unoccupied habitat from many sites along the LWR, although the rationale for multiple preserves differs depending on the species under consideration.

Hypericum cumulicola has a high degree of differentiation among populations. Over 73% of the isozyme variation in the species is found among populations, and we have evidence of little or no interpopulation gene flow. Although isozymes are neutral markers, the underlying assumption of their utility in conservation studies is that

the level of variation detected at marker loci directly reflects the level of variation that influences fitness (Milligan, Lebens-Mack, and Strand, 1994). That is, they reflect the genetic resources necessary for short-term ecological adaptation and for long-term evolutionary change. Significant positive correlations between isozyme variation and quantitative morphological traits that affect fitness have been demonstrated in plants (e.g., Ouborg, van Treuren, and van Damme, 1991; van Treuren et al., 1991).

Therefore, to preserve extant variation in *H. cumulicola*, many populations must be protected from across the small geographic range of the species to ensure retention of allelic and genotypic diversity. Because a large proportion of the variation exists among populations, even small populations are worth preserving.

Given the evidence from other studies (Quintana-Ascencio, Dolan, and Menges, 1998) of metapopulation dynamics in *H. cumulicola*, the high F_{ST} value of 0.724 may not simply reflect populations that are not interconnected by gene flow. Local populations that are connected by extinction and recolonization will also have high values of F_{ST} (if colonists come from a few source populations), and these two forms of demographic interconnectedness are difficult to distinguish using marker data alone (Milligan, Lebens-Mack, and Strand, 1994). Since we cannot predict which currently occupied sites might be extirpated and which unoccupied sites might be colonized, preservation of large areas of suitable habitat for *H. cumulicola* is also warranted.

Liatris ohlingerae with scattered, low-density populations and genetic structure consistent with a greater degree of outcrossing than the other two species may face additional challenges to its long-term persistence. This species may be more sensitive to negative effects of inbreeding due to decreased population size and numbers brought about by loss of habitat or changes in historical interpopulation gene flow (Barrett and Kohn, 1991). Preservation of large contiguous tracts of scrub would offer the best chances of successful conservation.

The rarest plant, in terms of numbers of occurrences, is *Eryngium cuneifolium*. Although some sites contain thousands of plants, there are only 20 known populations. Opportunities for long-distance seed dispersal are limited, and newly established populations in apparently suitable habitat have not been observed. Although populations are not particularly distinct from each other genetically, there are so few populations that none can afford to be lost. As noted by Godt and Hamrick (1996), when populations of a rare plant all occur in a small geographic area, they are extremely vulnerable to local catastrophes, such as drought. *Eryngium cuneifolium* appears to be among the most sensitive of all Florida scrub endemics to fire suppression (Menges and Kimmich, 1996), with local extirpations observed only 20–30 yr postfire.

Further studies are underway to directly document the breeding systems and pollinators of these species. Along with further investigation of metapopulation dynamics and long-term demographic patterns, these data will be integrated into a management plan to meet the goal of preserve design that optimizes conservation of these Florida scrub endemics, with their different levels and patterns of genetic variation.

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